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MUTATION IN ŒNOTHERA

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INTRODUCTORY

I HAVE been for some time interested in tracing the history of the various species and races of *Œnothera* from the early records of their introduction into Europe. This method is accompanied with many difficulties which only those know who have attempted it. Conclusions which seem justified in the light of the data in hand sometimes require modification when further records are examined. In a previous note in *Science* ('10), and especially in a longer paper ('11*a*) since published, I have brought together much of the data on which our knowledge of the early introduction of these forms into cultivation must rest.[1] Since that time I have been able to supplement those data by an examination of further records, and particularly of some of the type specimens of these plants in European herbaria. These have confirmed some of my previous conclusions and necessitated modifications of others. Herbarium specimens, where available, are of course the final court of appeal concerning the characters of any plant, but unfortunately they are not infrequently incomplete or even entirely lacking. My examination shows that probably a number of *Œnothera* races existed two or three

[1] Hill ('11) has also briefly discussed the subject and added some data.

centuries ago which are not known to occur in America to-day.

The *O. Lamarckiana* of de Vries's cultures is not the only *Œnothera* which is no longer known to be wild in this country. The same is true of the "European *biennis*" so-called, and of a race of *O. biennis* having very crinkled leaves, which I have cultivated from the Chelsea Physic Garden. It is not sufficiently kept in mind that the collector or species-maker necessarily abstracts. One form, or at best a very few, are selected for seeds or for description as types, from a population containing often a large number of closely allied races; for nature does not select between these races unless the differentiating characters are of value in the survival of the organism, and this appears often not to be the case. In this manner two or three centuries ago various races of *Œnothera* were selected and taken to Europe to be propagated in botanical gardens, but it is evident that many more races were left behind, and since the incoming of civilization some of these have probably disappeared. In nature, among open-pollinated (allogamous) plants (and presumably among a great many animals) there is no such thing as a "pure" species which will breed true in all its characters, showing only purely fluctuating variability. It is only by selecting and inbreeding for a few generations, that we get "pure lines." The only pure lines in nature are to be found among strictly self-fertilized (autogamous) forms. This idea, which has been emphasized by Cook ('07), seems to be too frequently lost sight of in evolutionary studies. The pure line, while a valuable and necessary means of analyzing various problems of heredity, is essentially a laboratory product seldom duplicated in nature among allogamous plants. By continued inbreeding and selection to smaller and smaller differences, races which are more and more uniform may be obtained, as the "pure line" work tends to show. But the natural wild species must (unless regularly self-fertilizing) be looked upon

as an intercrossing population of races, whose appearance is ever changing (within limits) from generation to generation, according to the particular series of crosses or selfings which happen to occur in each generation. Some of the races are likely to fluctuate in numbers or be dropped out entirely as conditions change. The way in which the face of the population changes from one generation to another will, of course, depend upon how the character-differences are inherited, but we need not consider that question here.

It therefore seems to be idle to inquire whether in this sense crossing of the allogamous œnotheras, such as *O. Lamarckiana* and *O. grandiflora,* has taken place, for we must assume that it *has* occurred, in the wild condition as well as in gardens. Our "species" (particularly the earlier ones, when less fine distinctions were drawn than now) are founded upon certain chance combinations resulting from such crosses, which have attracted attention and been abstracted and rendered uniform by continued self-pollination. Nature herself is oblivious of the boundaries between "species" so long as, when crosses occur, the progeny are fertile, and this is frequently the case in *Œnothera.*

I am greatly indebted to Dr. B. Dayton Jackson, general secretary of the Linnæan Society, for the privilege of examining the type specimens of Linnæus's "Species Plantarum," and to Dr. A. B. Rendle and his colleagues of the British Museum (Natural History) for courtesies in connection with the examination of extensive *Œnothera* collections, including the plants of Linnæus's "Hortus Cliffortianus" and various early American collections.

The species of *Œnothera* which need particularly to be accounted for are what we now know as *O. muricata* L., *O. biennis* L., *O. Lamarckiana* Ser. and *O. grandiflora* Ait. Each of these "species" is really an aggregation of a large number of races, differing in many characters but having certain features in common. It

becomes a question how many of these races are to be included in each "species," and it is often a purely arbitrary matter whether the line between two of the species shall be drawn so as to include certain races in one or the other.

As an instance of this I may cite the case of *O. biennis* L. and *O. muricata* L. I have cultivated many wild races of both, including races of *O. muricata* from such localities as Woods Hole, Mass., Gay Head, Mass., Seal Harbor, Me., Middleton, N. S., St. John, N. B., Winnipeg, Man., and St. Paul, Minn. Certain of the races, for instance from St. John and Winnipeg, appeared to be identical, but in most cases they produced uniform races differing constantly in such features as width and color of leaves (varying in different races from very narrow to very broadly lanceolate) and average height of the plant, as well as other characters. The only feature in which all agreed was in certain flower characters, all having a smaller flower than *O. biennis*. In most cases the leaves are also narrower than in *O. biennis,* but as certain races having smaller flowers than *O. biennis* also have broad leaves, it becomes an arbitrary distinction whether these races be included in *O. biennis* on the basis of their broad leaves or in *O. muricata* on the basis of their smaller flowers. The latter course has been followed and they are accordingly classed as *O. muricata* races. On this basis, the only distinction between *O. biennis* forms and *O. muricata* forms is in the size of the flowers, and even this distinction is an arbitrary one. I will not discuss in this connection certain interesting questions relating to the geographical distribution of these races.

My cultures have similarly isolated a number of races of *O. biennis,* some of which differ from each other in most unexpected characters. There is a wide range of variation in flower-size in the different races of *O. biennis,* as there is also to a less extent in *O. muricata.* The general distinction is usually drawn, that self-polli-

nating forms (*i. e.*, those having a short style so that the anthers surround the stigma in the bud) shall be classed as *O. biennis,* and forms with a long style, hence open-pollinated, shall be included in the *O. Lamarckiana* or *O. grandiflora* series of forms. Yet *O. Simsiana* Ser. is a species having large flowers and a short style. The "European *biennis*" has flowers which are larger than any known American races, but it is conveniently classed as *O. biennis* on the basis of its short style. The question as to the characters of the particular plant on which the species name was originally based, also of course enters here. In connection with the early records, herbarium specimens and figures are the chief means of determining approximately the race to which a plant under a given name belonged. The present paper contains the writer's further conclusions concerning these various races and species, and the reader will constantly be referred in this connection to the extensive data already brought together in the paper previously mentioned (Gates, '11*a*).

Early Records and Herbarium Specimens

We may now consider the identity of these various forms in succession. In the paper just mentioned I have given the nine species of *Onagra* listed by Tournefort in his "Institutiones Rei Herbariæ," 1700. Of these the first five are œnotheras. Species number five, *Onagra angustifolia, caule rubro, flore minori,* I have already concluded (*loc. cit.*, p. 87) is our present *O. muricata* L., on the basis of Barrelier's figure (*Lysimachia angustifolia, spicata, lutea, Lusitanica,* fig. 990 in "Plantæ per Gall., Hisp. et Italiam observatæ," 1714). This conclusion is now shown to be correct by Plukenet's figure in the "Almagestum" under the name *Lysimachia lutea, corniculata, angustifolia, flore minore* (t. 202, f. 7), which represents a small-flowered *Œnothera* with narrow leaves. The final proof is given by an examination

of the specimen (probably the one from which the figure was drawn) in Plukenet's "Herbarium," Vol. 96, f. 167, which is in the British Museum. The flowers of this specimen are much smaller than in *O. biennis* and the leaves are narrow, making it evidently a race of *O. muricata*. Linnæus afterwards (quite incorrectly) ("Sp. Pl.," p. 346) combined it with his species *O. fruticosa*. A type of the latter species is a specimen collected by Clayton in Virginia, and is from the herbarium of Gronovius in the British Museum. It represents a race of the modern *O. fruticosa* L. That the error of combining Tournefort's species with this was afterwards recognized is shown by the fact that in an annotated copy of the "Species Plantarum," 2 edition, 1762, in the possession of the Linnæan Society, the citation of "*Onagra angustifolia, caule rubro, flore minore* Tournef. inst. 302" under *O. fruticosa* L. is crossed out. Type specimens of both *O. fruticosa* and *O. muricata* for the "Species Plantarum" are to be found in the Linnæan Herbarium. The latter differs from the type specimen of *O. biennis* (which will be referred to later) in having somewhat smaller flowers, more numerous long hairs on the sepals, narrower and more pointed leaves, and numerous conspicuous murications (long hairs arising from papillæ) on the stem.

We may now take up the consideration of Tournefort's first three species and their synonyms. In my former paper I was strongly of the opinion that species (I) represented a plant which was more closely related to *O. Lamarckiana* than to *O. biennis,* although not identical with any known form, except possibly *O. lævifolia*. The large flowers and quadrangular buds, as well as a consideration of the synonymy, seemed to demand that it be placed with the *O. Lamarckiana* series of forms, rather than with *O. biennis* or *O. grandiflora*. A subsequent examination of certain early specimens has thrown doubt upon this opinion. I have shown (*l. c.*) that the

Lysimachia lutea corniculata of Bauhin,[2] which Tournefort cites as a synonym for his *Onagra latifolia,* is the same plant, or at any rate the same description, as Morison's *Lysimachia lutea corniculata non papposa* and Ray's *Lysimachia lutea Virginiana.* The crucial point in this early synonymy seems to be in Barrelier (1714), who gives rather accurate figures of three species of œnothera, together with their synonymy (see Gates, '11*a,* p. 102). His species (1) is quite certainly a race of *O. biennis,* his species (2) is with equal certainty a race of *O. muricata,* and (3), which has much larger flowers, must, I think, belong somewhere in the series of large-flowered forms represented by *O. grandiflora* and *O. Lamarckiana.* The fact that the name *Lysimachia lutea, corniculata, latifolia, Lusitanica* under which Barrelier figures his species (3) is almost identical with the name *Lysimachia Virginiana latifolia, lutea, corniculata* under which Morison figures *his* large-flowered form (Fig. 7), made it probable that Barrelier's species (3) referred to the same plant as Morison's figure. However, this can not be certain. But I regard it as quite certain that the plant figured by Morison (Fig. 8) under the name *Lysimachia Virginiana angustifolia, corniculata* (see Gates, '11*a,* p. 99) is *O. muricata.* The diameter of the flowers in his Fig. 7 is exactly three times that in Fig. 8. Now Gray's "Manual," ed. 7, gives the length of petals in *O. muricata* as 12–20 mm., in *O. biennis* as 15–25 mm., and in *O. grandiflora* as 40–60 mm., so that the flowers of *O. grandiflora* (or *O. Lamarckiana*) would be approximately three times the diameter of those in *O. muricata,* while even the "European *biennis*" could scarcely reach these dimensions. This appears to be an additional reason for supposing that Morison's larger-flowered plant came in the series represented by

[2] On inquiry from Professor A. Fischer, director of the Botanische Anstalt, Basel, Switzerland, where Bauhin's Herbarium is kept, I find that the specimen of *Lysimachia lutea corniculata,* along with about two thirds of his collection, was discarded as spoiled when the Herbarium was renovated several years ago.

O. grandiflora and *O. Lamarckiana* rather than in *O. biennis,* but as already stated, an argument of this nature can not reach finality. Whether Morison's Fig. 7 represents one of the *grandiflora-Lamarckiana* series or the "European *biennis,*" it seems certain that Barrelier's species (3) came in the large-flowered, open-pollinated series represented by *O. grandiflora* or *O. Lamarckiana.*

Unfortunately, the actual specimens in the British Museum, which bear these early names of Tournefort and are supposed to have served as the types for the "Hortus Cliffortianus," are not fully authenticated. The handwriting is said not to be that of Linnæus, and certain differences between the names employed and those which Linnæus himself would probably have used, seem to indicate that they were written by an amanuensis or that some mistake occurred in the naming. This deprives us of certainty in regard to the names they bear. The characters of the specimens themselves are very well preserved. The first specimen (which I shall refer to as specimen 1) bears on the label the name "*Onagra latifolia flore sulphureo*"; the second specimen (2), "*Onagra latifolia.* T. 302," and beneath it is written "*Œnothera octovalvis.*" But *O. octovalvis* was a species of Jussieua. These two specimens are identical in every character. They represent evidently a race of the "European *biennis*" having larger flowers than American forms of *O. biennis,* though not so large as *O. Lamarckiana.* The style is short so that the stamens surround the stigma, the buds bear some long hairs, red papillæ occur on the stem, and the leaves are rather broadly lanceolate. The stigma lobes are remarkably long in all the flowers on both specimens. These two specimens may have served as the types of Linnæus's species (1) in Hort. Cliff. (see Gates, '11*a,* p. 102). As far as the characters of these specimens are concerned, they really resemble *O. Lamarckiana* more than they do the American races of *O. biennis,* but are classed with *O. biennis* because the flowers are self-pollinating.

The next specimen (3) in this series is one bearing the label *Onagra latifolia, flore dilutiore* T. 302. As a matter of fact, it differs remarkably little from the two specimens just described. The leaves and stem show no visible difference at all, but the petals appear to have been slightly smaller. The flowers differ markedly, however, in having longer styles, so that the stigma projects some distance beyond the stamens. The stigma lobes are also very short, differing conspicuously in this respect from those of the specimens above. This specimen is something of a puzzle. It was apparently open-pollinated because of its long styles. Yet its flowers were no larger than those of the "European *biennis*." It shows that races may have existed and disappeared, which were quite different from anything we know at present. Whether this form shall be classed with the "European *biennis*" on account of the size of its flowers, or with *O. Lamarckiana* on account of its long style, appears to be an arbitrary matter. Such specimens serve to show that the range of "variability" of these œnotheras in certain directions may have been formerly much greater than would be supposed from a study of those races which have survived to the present day.

Another interesting specimen (4) in this collection is one marked *Onagra latifolia* Tourn. with the date 1743 and a number, 1082. I am indebted to Dr. Rendle for the explanation of the history of this specimen. Sir Hans Sloane contributed to the Herbarium of the Royal Society each year for a number of years, fifty specimens from plants grown at the Chelsea Physic Garden, and these were numbered consecutively. This plant was therefore grown in the Chelsea Physic Garden in 1743. It is apparently the same as specimens (1) and (2) already described as probable types for the "Hort. Cliff." Some of the stem leaves have short petioles and sloping base, others are apparently sessile with broadened base.

The next specimen (5) has the same history as the last. It bears the date 1779 and the number 2878. The

label reads "*Œnothera biennis* foliis ovato-lanceolatis planis, caule muricato subvilloso Lin.: Spec. Plant. 492. *Lysimachia lutea corniculata.* Bauhin: pin. 245." This specimen has smaller flowers than the previous ones, the flowers being the same size as the American races of *O. biennis.* The leaves are very broadly lanceolate, sharply narrowed at base to a very short petiole, and appear to be of a different shape from those of any American *biennis* I have seen. The stem bears scattered papillæ from which long hairs arise.

A consideration of these five specimens makes it highly probable that Tournefort's *Onagra latifolia* and Bauhin's *Lysimachia lutea corniculata* belonged to what we now for convenience call the "European *biennis*" rather than to the larger-flowered, longer-styled, *O. Lamarckiana.* Yet specimen (3) with its long style though the flowers are the same size as in the European *biennis,* makes it impossible to be dogmatic as to where the line is to be drawn between the *O. Lamarckiana* and the *O. biennis* series of forms. If these specimens are correctly labeled, then there must have been comparatively little difference between Tournfort's species (1) and (2), (1) representing the "European *biennis*" and (2) a form probably open-pollinated but with flowers smaller than the present *O. Lamarckiana.* The "long and narrow pale green leaves" of Bauhin's and Parkinson's plant (see Gates, '11*a,* pp. 91 and 95) would indicate that it differed in certain features from any race of the European *biennis* now known.

As already pointed out, the synonymy as well as the flower-size would indicate that Morison's larger-flowered plant *Lysimachia Virginiana latifolia lutea, corniculata* was the same as Barrelier's *Lysimachia lutea, corniculata, latifolia, Lusitanica* which is undoubtedly a large-flowered form. However, it seems on the whole more probable that Morison's plant was the same as Bauhin's, whose description he copies. In any case it seems clear that Barrelier's *Lysimachia lutea, cornicu-*

lata, latifolia, Lusitanica was a large-flowered form belonging in the *grandiflora-Lamarckiana* series, and there is no reason to doubt that his citation of Tournefort's *Onagra latifolia, floribus amplis* as a synonym is correct. It is therefore highly probable that Tournefort's species (3) represents *O. grandiflora,* or perchance *O. Lamarckiana* or some race between these two as we now know them.

The type specimen of Linnæus's *O. biennis* in the "Species Plantarum" (to be found in the Linnæan Herbarium) is, however, not the "European *biennis,*" but a smaller-flowered form representing one of the American races of *O. biennis,* having rather narrowly lanceolate stem leaves. I have already pointed out ('11*a,* p. 104) that Linnæus does not cite figures of this form in his synonymy, although a good figure by Barrelier was in existence. Instead he cites Morison's figure which now appears most probably to have been the "European *biennis,*" and in the "Hort. Cliff." he cites Barrelier's figure of *Lysimachia lutea corniculata latifolia lusitanica,* which was undoubtedly a large-flowered form.

To summarize briefly the conclusions which seem justified from all the available data, it appears that the earliest introduction, as represented by the plants of Bauhin, Parkinson, Morison and Ray, belonged to a race of what we now know as the "European *biennis,*" having flowers larger than the present American races but self-pollinated, although an open-pollinated form with long style appears also to have occurred (specimen 3). *O. muricata* was recognized by Tournefort in 1700, and both *O. muricata* and the "American *biennis*" were figured by Barrelier in 1714, in addition to a large-flowered species which must have been related to *O. grandiflora* or *O. Lamarckiana.* This large-flowered form appears to have been first recognized and briefly described by Ray in 1686 (see Gates, '11*a,* p. 100). Different hypotheses as to the relation between *O. grandiflora* and *O. Lamarckiana* will be considered later in this paper.

O. grandiflora Ait.

In a previous paper ('11*a*, p. 110) I reproduced the manuscript of L'Heritier's description of *O. grandiflora,* which was written about 1788 but was never published. The type specimen of *O. grandiflora* in the British Museum was grown in the garden of Dr. Fothergill in 1778. It has narrowly lanceolate leaves and slender hypanthia, agreeing exactly with some of the plants in my cultures of *O. grandiflora* from Alabama. Solander really did the descriptive work upon this form, and the species should have been given his name instead of that of Aiton. In Vol. IX, p. 387, of the Solander manuscripts, which are in the British Museum, he gives the following additional notes on this plant of Bartram and Fothergill: "Œnothera grandiflora foliis lanceolatis denticulatis villosiusculis, petalis cuneiformibus, calycibus aristatis, pilis caulinis basi tuberculosis. Habitat in America septentrionalis prope Mississippi. Bartram Junr." These characters serve further to identify the plant with the present *O. grandiflora,* the words "petalis cuneiformibus" and "calycibus aristatis" being particularly distinctive.

Evidence from Later Herbarium Specimens.—I may now refer to a number of specimens in the British Museum, which are of special interest for one reason or another. The first of these specimens was marked "*Œnanthera grandiflora* Lin: Willd.," the species name being crossed out and "*longiflora*" written above it. On the back of the page is written "Herb. Demidoff. Pallas." This applies to plants grown by Demidoff in his garden, founded at Moscow in 1756. This specimen differs from the type specimen of *O. grandiflora* in having larger stouter buds, very much stouter hypanthia, larger flowers, leaves narrow but shorter than the type of *O. grandiflora.* It appears to resemble *O. rubrinervis* more than any other form, but has stouter hypanthia than I have ever seen in this mutant.

Another specimen bears the following label: "Bar-

clay. *Œnothera* sp. Shrubby, 3 feet high, flowers yellow. Hab. hilly. Bodegas." This plant from Ecuador has flowers the size of *O. Lamarckiana,* many long hairs on the sepals and young leaves, the leaves being rather narrowly lanceolate, petiolate. The plant must have been very much like *O. rubrinervis,* though differing somewhat in leaf characters. Ecuador is an unexpected place to find plants having these characters.

A very interesting sheet bears the name *O. biennis* L. var. *muricata* Torr. & Gray. It was collected by Dr. Wm. M. Bell, of London, in the Raton Mountains (which extend from southern Colorado to New Mexico) in 1867. There are two specimens and several extra flowers and buds. The flowers are as large as those of *O. Lamarckiana,* the style is long so that the flower is open-pollinated; the hypanthium and bud cone bear numerous long hairs; the buds are the precise size and shape of *O. rubrinervis;* the stem leaves are more narrowly lanceolate than *O. Lamarckiana* but are often broad and sessile at base like that form. This plant is strikingly like *O. rubrinervis* in every particular, except that the upper stem leaves are perhaps a little narrower. The presumption is that these plants were collected in the wild condition, and I have found no reason for supposing otherwise. This would seem to support the view that these *Lamarckiana* forms were formerly found wild in the western region, although it has been suggested that the Texas plants, from which de Vries's cultures appear to have originated, were perhaps descended from garden seeds.

Another very interesting specimen is marked "*Onagra guttata* Greene n. sp., New Mexico, 1904. Alt. 6600 feet." Its leaves are very narrowly lanceolate (much narrower than *O. lævifolia*); the stems red, with many red papillæ bearing long hairs; the flowers are large, style long, and there are many long hairs on the sepals, which also have red bands like *O. rubrinervis.*

These specimens show that forms having large flow-

ers, which belong in the *O. Lamarckiana* series, occur in the western region. One of these specimens is scarcely if at all distinguishable from *O. rubrinervis*. Contrary to the opinion sometimes expressed, I have found herbarium specimens of great value in determining the exact characters of many of these races. There would be no excuse for one familiar with the characters of the plants from cultures, failing to discriminate easily between, for example, *O. grandiflora* and *O. Lamarckiana*, from herbarium specimens showing merely a flowering shoot. And much less conspicuous differences than these, for example in the width or shape of leaves, can be determined with equal accuracy. For example, no one who is familiar with the plants in cultures would confuse typical herbarium specimens of *O. Lamarckiana* and *O. rubrinervis*.

Hypotheses Concerning the Origin of O. Lamarckiana.—There has long been a disposition to look upon *O. Lamarckiana* as a "hybrid"[3] and to suppose that, on this account, the phenomena of the sudden appearance of aberrant types (as described by de Vries), displayed by this form, are necessarily deprived of evolutionary significance. This latter view is one which I do not share. As already pointed out, I consider it necessary to regard open-pollinated forms as hybrids in the sense that their immediate ancestry has been participated in by many races differing in various characters. The germ plasm of such forms is like an unpurified chemical or mixture of chemicals and can only be "purified" by continued self-pollination. This "impure" condition is the one under which the evolution of open-pollinated plants or interbreeding animals goes on, and any assumption

[3] It might be pointed out that the flower characters (which are the crucial characters in many *Œnothera* crosses) of the "European *biennis*" are such as might be expected if it were a "hybrid" between some race of the American *biennis* and some large-flowered form in the *O. Lamarckiana* series. Perhaps it originated as such a hybrid, but the contemplation of the fact is, in itself, of little value for the study of progressive evolution. For practical evolutionary studies, the only universal criterion of a species must be that it breeds true to its peculiarities.

to the contrary merely distorts the facts. If it be assumed that *O. Lamarckiana* is the sudden product of a single cross between two rather more widely separated species, the situation is slightly though not fundamentally changed. As regards *O. Lamarckiana,* the only forms we know which could reasonably be supposed to be its ancestors in this way would be *O. biennis* and *O. grandiflora,* as I have already pointed out (Gates, '11*a,* p. 119). There have doubtless been plenty of opportunities for these species to cross in Botanical Gardens and they have doubtless done so, since the evidence seems clear that certain races belonging to these two "species" were recognized as early as 1686 by Ray as under cultivation.[4] But these species both came from the Virginian region, where there is ample evidence that *O. grandiflora* as well as *O. biennis* originally grew wild, and where the former species was commonly found as late as 1820 (Barton's "Flora of North America," plate 6). Under these circumstances there must have been plenty of opportunities for *O. grandiflora* to be pollinated from *O. biennis* (these forms are visited by moths in the evening when the flowers open), and it would be a bold assumption to suppose that such crosses had not taken place centuries before the white man came to America. Hence if this were the manner of origin of *O. Lamarckiana,* it must have originated in nature long ago. Of course it is well-known that many such species-hybrids are sterile so that when they occur they fail to bridge the gap between species or to take any part in those species' subsequent history and evolution. Assuming that *O. Lamarckiana* originated in this way, its fertility makes its presence in the population of forms of equal im-

[4] I have grown cultures of œnotheras from nearly all the European botanical gardens. The self-pollinating forms are generally quite uniform, while the open-pollinating forms frequently show much variability, which is evidently in part at least the result of crossing. My cultures of *O. grandiflora* from its wild locality in Alabama also show that it contains various aberrant types. On the other hand, it is also true that the self-pollinating *O. biennis* in some localities contains more than one type, but in the case of *O. biennis* it is not probable that these types have arisen through crossing.

portance with that of the two parent species, for it will take an equal part in producing descendants. Furthermore, crossing between the new hybrid forms and the parents will go on indefinitely, producing a host of interbreeding races, and this population will constitute the material for further evolution.

I have been studying this process by means of cultures from seeds of plants on the sand dunes near Liverpool, England, where *biennis, Lamarckiana* and *grandiflora* have been interbreeding freely for at least a century, producing a host of races (including several of the mutants of *O. Lamarckiana*), some of which split, but many are found to breed true for at least two generations. It seems to me that the question to ask regarding these races is not as to whether they have originated in connection with crossing, for it is certain that they have originated at least in the presence of conditions in which crossing is taking place in every generation. The question is rather what relation (if any) these races bear to the previous evolution of these forms, whether any of them are progressive in the sense that they will supplant the other races and become the progenitors of future generations, to the exclusion of those which were formerly progenitors. In other words, are the new races progressive in the sense that they show some further development of any character or some new departure in comparison with the parental types, and are they also capable of surviving, propagating themselves and ultimately becoming important elements of the population, from which new races may in turn develop? Does crossing ever lead to the appearance of new and progressive types by the disturbance it produces in the germ plasm, rather than by the mere combination and redistribution of the characters of the forms it brings together? Or is mutation a process apart from any germinal disturbance resulting from crossing? The answers to these questions are often very difficult, but upon these answers depends in large part the status which will ulti-

mately be given to the mutation phenomena in *O. Lamarckiana* as an evolutionary factor.[5]

Is O. Lamarckiana obtained from O. grandiflora × O. biennis?—Before pursuing further the subject of the cause of the mutations in *O. Lamarckiana*, let us examine the hypothesis that *O. Lamarckiana* is the result of a direct cross between *O. biennis* and *O. grandiflora*, for while, since *O. Lamarckiana* must be assumed to have undergone crossing in any case, it is not of vital significance just what those crosses may have been, yet it would be of interest if it could be shown that *O. Lamarckiana* has arisen and can be synthesized, as the result of a single cross. Davis ('11) has recently attempted to produce *O. Lamarckiana* in this manner. His descriptions, however, fail to state the points in the characters of his hybrids, which any one who is familiar with these plants would like to know. Particularly does he omit to state how the bud characters of his hybrids differ from those of *O. grandiflora*. It is stated that the hybrids are in general intermediate between the parent species. This would be expected, at least as regards the flower characters, from the behavior of other hybrids in œnothera, *e. g., O. Lamarckiana × O. biennis*. The flower characters in this cross are nearly intermediate, though resembling *biennis* more than *Lamarckiana*. I have observed closely the flower characters of many crosses, including hybrids between series of forms belonging respectively to *O. grandiflora* and *O. Lamarckiana*, and the flowers are usually intermediate in their characters, though sometimes nearer one parent than the other. If the flowers of Davis's cross are also

[5] It might be assumed that *O. biennis* and *O. grandiflora* were the original forms to become naturalized on the English sand dunes, and that *O. Lamarckiana* has since appeared as the result of crossing between these races. If this is the case, then *O. Lamarckiana* (and many related races which have resulted from further crossing and mutation) has since been successful, under the new conditions, in supplanting the parent forms to a large extent. We should, therefore, in any case, expect these *O. Lamarckiana* forms to become the progenitors of the future generations, and to determine in greater part the future evolution, whatever that might be.

a blend of the parents, as he states ('11, p. 213), then they can not be the same as the flower characters of *O. Lamarckiana*. If, on the other hand, the flowers are as he states, "scarcely distinguishable from those of *O. Lamarckiana*," then they are not a blend of the parental characters.

I have previously pointed out the differences between *O. grandiflora* and *O. Lamarckiana* (Gates, '99*a*, pp. 131, 132) and Miss Vail (in MacDougal, Vail and Shull, '07, p. 66) has described the characters of *O. grandiflora* in detail. For convenience, the flower differences between *O. biennis*, *O. grandiflora* and *O. Lamarckiana* may be summarized here. *O. biennis* has small flowers, in which the stamens surround the stigma in the bud. The anthers are in contact with the stigma in the bud and are ruptured before the bud opens, so that when the opening of the flower occurs, and the anthers move away from the stigma, viscous strings of pollen are found running from each anther to a lobe of the stigma in the newly opened flower. Self-pollination thus invariably takes place in *O. biennis*. In neither *O. Lamarckiana* nor *O. grandiflora* does this happen, for the reason that the style is longer so that the stigma lobes, instead of being surrounded by the anthers, are projected above them. The anthers are ruptured as early as in *O. biennis*, but not being in contact with the stigma lobes, the strings of pollen seen in the opening *biennis* flower never occur in *O. Lamarckiana* or *O. grandiflora*. If, as Davis states (see *l. c.*, p. 216), the anthers in *O. Lamarckiana* touch the lower part of the stigma lobes, then these strings of pollen and self-pollination would occur. But this condition is not found in *O. Lamarckiana*, though it does occur (as would be expected) in the hybrid *O. biennis* × *O. Lamarckiana*.

As regards the size of the flower, the statements of Davis also need some revision. He assumes that the flower of *O. Lamarckiana* is smaller than that of *O. grandiflora*, whereas the *O. Lamarckiana* of my cultures

is on the average somewhat larger than *O. grandiflora* from Alabama grown under the same conditions. The same thing is shown by the measurements of Miss Vail. I should first point out that in all the œnotheras the flowers in the early part of the season are uniform in size, but towards the latter part of the blooming-season, with dwindling vitality they steadily decrease in size until the latest-blooming flowers in *O. Lamarckiana,* for example, have petals no larger than *O. biennis.* The style in *O. Lamarckiana* does not, however, decrease in length at as fast a rate as the petals, the result being that in late-blooming flowers it not infrequently protrudes from the unopened bud. But there is no time in *O. Lamarckiana* (in my cultures) when the "base of the stigma lobes is slightly below the tips of the anthers." Davis's Fig. 18 ('11) is misleading as a typical flower of *O. Lamarckiana,* its petals being much too small. He states (p. 216) that the hybrid whose flowers are "scarcely distinguishable from those of *O. Lamarckiana*" has petals 2.2 cm. long. By choosing flowers towards the end of the blooming-season it will be possible to find petals of any desired size, down to that of *O. biennis* itself, but in stating the size of petals for comparison with *O. grandiflora,* it is only fair to choose the typical flowers which are characteristic of the greater part of the season, and which *O. biennis* never produces. MacDougal ('03) states the length of the petals in *O. Lamarckiana* to be 4–5 cm., and Miss Vail in *O. grandiflora* ('07, p. 66) 3.5–4.0 cm., which agrees with my cultures, while in Gray's Manual the petals of *O. grandiflora* are given as 4–6 cm. In my cultures the flowers of *O. Lamarckiana* have been certainly not smaller, but on the whole larger, than in *O. grandiflora. O. Lamarckiana* is therefore not intermediate between *O. biennis* and *O. grandiflora,* either in length of style (though the style may sometimes be *slightly* shorter than in *O. grandiflora*) or size of petals, but is almost in agreement with *O. grandiflora* in both these characters. As already pointed

out, the petals of *O. grandiflora* are also characteristically narrower and more cuneiform than in *O. Lamarckiana,* though this is not always the case.

In a number of other flower characters *O. Lamarckiana* is more in agreement with *O. biennis,* and contrasted with *O. grandiflora.* Both the first-named species have quadrangular buds with a prominent median ridge on each sepal, while in *O. grandiflora* the buds are rounded and the median ridge much less prominent. Also these two species agree in bearing on the sepals, hypanthium and ovary a conspicuous long, pointed type of trichome arising each from a papilla and giving the bud a rather strongly pubescent appearance;[6] while this type of hair is, in my experience, always absent from the buds of *O. grandiflora,* which therefore have a glabrous appearance, although a small inconspicuous type of hair is often present, as is the case always in the other two species. *O. biennis* and *O. Lamarckiana* also agree in having rather thick sepals and rather stout sepal tips, while in *O. grandiflora* the sepals are thinner and more delicate, and the sepal tips longer and more setaceous. These differences give the buds of *O. grandiflora* a very different appearance from those of *O. Lamarckiana,* so that even in ordinary herbarium material there is not the slightest difficulty in distinguishing them.

These contrasting flower characters are brought together for greater convenience of reference, in the table below:

FLOWER CHARACTERS		
O. biennis	*O. Lamarckiana*	*O. grandiflora*
Petals 12–16 mm. long.	Petals 40–50 mm. long.	Petals 35–40 or 60 (?) mm. long.
Stigma surrounded by the anthers, invariably causing self-pollination before the bud opens.	Stigma lobes above the anthers, so that self-pollination in the bud does not occur, though the style may be *slightly* shorter than in *O. grandiflora.*	Stigma lobes above the anthers, so that self-pollination in the bud does not occur.

[6] In some races of *O. biennis* there is instead an intermediate type of trichome arising from the even surface of the buds.

Buds quadrangular.	Buds quadrangular.	Buds rounded.
Buds bearing two types of hairs, (1) a short, delicate type, (2) a long, pointed type arising from papillæ and giving the bud a pubescent appearance.	Same as *O. biennis.*	Buds bearing only type (1), or sometimes entirely free from hairs. Type (2) is never seen to occur on the buds of this form, unless previously crossed with *O. biennis* or *O. Lamarckiana.*
Sepals rather thick and sepal tips rather stout.	Essentially the same as *O. biennis.*	Sepals thinner and sepal tips more setaceous.

Thus *O. Lamarckiana* agrees with *O. biennis* in certain features of the flowers, while agreeing equally with *O. grandiflora* in certain other features. We know that these three species when crossed give more or less blended or intermediate hybrids, as appears to be frequently the case in crosses between "Linnæan" species.[7] This being the case, we should not expect to derive *O. Lamarckiana* from a cross between the ordinary races of *O. biennis* and *O. grandiflora,* for this would imply alternative rather than blended inheritance of the various flower characters. Davis has not taken into account the important differentiating features between the buds of *O. Lamarckiana* and *O. grandiflora,* merely telling us that the "inflorescence was very similar to *O. Lamarckiana,*" and that "the only essential difference between the buds lay in the slightly greater attenuation of the sepal tips." But his hybrids can not be, as he states, and as would be anticipated from the results of similar crosses in œno-

[7] In an extensive series of crosses between *O. Lamarckiana* and *O. grandiflora* races, the results of which can not be presented here, the flowers of the F_1 are shown to be, in many cases, at least, a blend of the parents. The buds are less conspicuously quadrangular than in *O. Lamarckiana,* the sepal tips more slender, and the long type of hair is about half as numerous. The casual observer would consider these buds to be the same as in *O. Lamarckiana.* Closer inspection, however, shows that this is not the case. In certain of these crosses, however, a type occurs in the F_1 having buds which closely resemble *O. grandiflora.*

thera, a blend of the parental characters, and at the same time agree with *O. Lamarckiana.*

Similarly, in the description of the foliage of his hybrids, Davis fails to take into account the leaf-differences involved. *O. grandiflora* agrees with most American races of *O. biennis,* in having stem-leaves which are lanceolate and tapering at both ends, forming a petiole. In *O. Lamarckiana* the stem-leaves are, on the contrary, usually sessile and broad, almost clasping, at the base, in addition to being crinkled.

A form which would resemble *O. Lamarckiana* much more closely than the hybrids of Davis, could doubtless be synthesized by using a race of *O. biennis* which I have cultivated from seeds obtained from the Chelsea Physic Garden. This race differs strikingly from any other race of *O. biennis* I have seen, in having stem-leaves sessile, very broad at base and very much crinkled. If such a race were crossed with *O. grandiflora,* hybrids might be expected whose foliage at least would closely resemble that of *O. Lamarckiana,* though the flowers would probably be intermediate between *O. Lamarckiana* and *O. biennis.*

One feature which has always made it appear improbable that *O. Lamarckiana* originated as the result of the single cross *O. grandiflora* × *O. biennis,* is the way in which the mutants of *O. Lamarckiana* all agree with that form in certain characters; and not one of them, so far as I am aware, shows any indication of a reversion towards either *O. biennis* or *O. grandiflora.* That the mutants all have certain features in common, which they do not share with *O. biennis* or *O. grandiflora,* and that all may be grouped around *O. Lamarckiana,* was shown in my analytical key to these forms (Gates, '09*a*, pp. 126, 127). While there are wide departures from *O. Lamarckiana* in many characters, in no case does this appear to bring them nearer either *O. biennis* or *O. grandiflora* races. It is difficult to understand why this does not occur, on the theory that *O. Lamarckiana* is such a

simple hybrid.[8] These facts that, so far as now known, *O. biennis, O. Lamarckiana* and *O. grandiflora* all behave alike in crosses with each other (that is, they give blends), together with the fact that none of the mutants revert towards either *O. biennis* or *O. grandiflora,* have always seemed unfavorable to the view that *O. Lamarckiana* has originated suddenly from such a single cross. On the other hand, it by no means follows that *O. Lamarckiana* or various other species of *Œnothera* could not be produced by sufficient crossing of races under suitable conditions. My studies of a colony of œnotheras from the English sand dunes, show that numerous races which breed true and have numerous entirely unanticipated characters (often differing from each other conspicuously in every organ) can be obtained as the result of indiscriminate crossing. Some of these races when crossed give blends and have thus far defied Mendelian analysis. I have been able to synthesize at least one of these true-breeding forms by crossing of races. A number of the other peculiar constant races have doubtless had a similar origin, though too complex to be easily repeated. The character-differences of these races do not *appear* to be Mendelian and the races come true except for varying percentages of "mutants."

The mutants of *O. Lamarckiana* themselves, when crossed with their parent form, show apparently a different type of behavior from the species, but that is a matter I will not enter into in the present paper.

How do the Mutants of O. Lamarckiana Originate?—Tower's experience ('10, p. 315) in crossing species of *Leptinotarsa* and thus synthesizing a new race which breeds true except for sporadic "mutants," appears to

[8] In my cultures of œnotheras from the sand dunes of the coast of England, I have obtained occasional mutants having many of the flower-characters of *O. biennis.* But in this case there was abundant opportunity for recent crossing with *O. biennis* to have taken place, and this would seem to be the most probable explanation of their occurrence. I have more recently seen similar occurrences in forms from botanical gardens which have obviously undergone much crossing.

be similar to the behavior just described, and increases the probability that *O. Lamarckiana* may have had a similar origin in nature and perhaps also in gardens. As already pointed out in this paper, it must be assumed that *O. Lamarckiana* has undergone crossing which has determined its present characters, and that its ancestry is therefore "impure." Whether it has resulted from any particular cross is of less interest from the evolutionary standpoint. As I have tried to show in the introduction to this paper, it probably must be conceded that the mutations of *O. Lamarckiana* are connected with previous crossing in the ancestry. This crossing was accompanied by a disturbance of the germ plasm, such disturbance manifesting itself in the occasional production of various aberrant types displaying whole series of new characters. But there are certain reasons why the resulting "disturbance" appears to be something more than a case of hybrid splitting. I shall not go into the details of this question in the present paper, but I may point out one or two facts. Even if (as is quite possible) certain mutants, such as *O. lata* and *O. nanella,* which are evidently retrogressive forms, could be so accounted for; there are at least two forms which could not be brought into this category. The first of these is *O. gigas* with its tetraploid number of chromosomes and a new series of characters, in part, no doubt, the result of the chromosome doubling. I ('09*b*) have suggested that this origin is probably similar to that of many tetraploid species in nature. Ordinary hybrid splitting will not account for it.

Another mutant which is clearly positive or progressive, and which can not be explained as a result of hybrid splitting, is *O. rubricalyx,* which appeared in my cultures in 1907 as a mutant from *O. rubrinervis,* showing a great increase in anthocyanin production (see Gates, '11*b,* for an account of its behavior). These two cases alone make it necessary to assume that "muta-

tion'' is due to a more general disturbance of the germ plasm than would occur in hybrid splitting.

The mutation process, therefore, while probably a result of previous crossing in the ancestry of *O. Lamarckiana,* is not a simple case of the splitting off or reappearance of types which entered into that ancestry. It is probable that much of the hybridization-behavior of the genus *Œnothera,* including particularly crosses which involve the mutants of *O. Lamarckiana* as one of the parents, will ultimately be harmonized with Mendelian categories.[9] But it is also probable that the appearance of the ''mutants'' of *O. Lamarckiana* is not a case of Mendelian splitting as we understand that process at present. The origin at least of such mutants as *O. gigas* and *O. rubricalyx* can not be explained on this basis, and at present can only be ascribed to a general disturbance or condition of instability, which probably resulted from previous crossing. The change in climate to which *O. Lamarckiana* has been subjected may also very well have had something to do with this disturbance, although this is less probable since this plant when brought back to America continues to exhibit the same mutation phenomena.

I have tried to show (1) that *O. Lamarckiana,* like other allogamous forms, has undoubtedly undergone crossing in its ancestry, and (2) that, whatever may have been the relation between these crosses and the appearance of mutants, the important matter to decide from the evolutionary standpoint is, Will these forms survive in nature and become the starting points for new races? As regards *O. gigas,* I have pointed out (Gates, '09*b*) many cases among plants, of species which have probably originated in an analogous manner.

There is one further phase of the mutation process

[9] A recent paper of Miss Saunders (''Studies in the Inheritance of Doubleness in Flowers—I, *Petunia,*'' *Journ. of Genetics,* I, 57–69, 1910) makes it probable that some at least of the alternative inheritance in crosses between *O. Lamarckiana* and its mutants will find an explanation in this way.

which I may touch upon very briefly. That is, the exact method of origin of the various mutants, from the cytological standpoint. It is now certain that the nature of the change involved is not the same in all cases. In the case of *O. gigas,* the most striking change, which brought with it many size changes, is the doubling in the chromosome number. This most probably occurred either in the fertilized egg or in the megaspore mother cell, which then developed apogamously (Gates, '11*c*). On the other hand it seems most probable that several other mutants are the results of changes occurring during the reduction divisions. All the retrogressive mutants may be accounted for in this way, as I have shown (Gates, '08), as the results of occasional irregularities in the distribution of members of the chromosome pairs, if we assume the chromosomes to differ in their chemical activities. *O. rubricalyx* again is a mutant from *O. rubrinervis* in which a marked *quantitative* change in one character (namely, capacity for anthocyanin production) has taken place. We have here the mutational appearance of a new dominant character. A change of this kind is not likely to be concerned with a new chromosome distribution, but is perhaps due to a cytoplasmic difference. As far as can be determined, the external conditions under which this mutant appeared and developed differed in no way from those of the rest of the culture, although it is impossible to deny that some local soil-difference might possibly have actuated this germinal change. This would, however, necessitate the assumption that the change took place in the germinating seed.

Mutation appears, therefore, to be not a simple unitary process of splitting, but to be the result of a condition of instability in the germinal material, which is again probably a result of previous crossing, and which leads to various types of departure from the parental race. That this process will account for much species-formation, and the polymorphism of many genera, can

not be doubted; but it is not clear that adaptation and the larger evolutionary trends can be sufficiently accounted for in this way, although occasional real germinal advances are seen to occur.

Summary

It must be assumed that crossing has taken place in the ancestry of *Œnothera Lamarckiana,* as well as in all forms whose flowers are open-pollinated. Among open-pollinated plants (and the same is probably true of animals) there is no such thing as a "pure" species, but rather, many interbreeding races whose combinations vary from generation to generation make up the population.

Further studies of historical records, and particularly of early herbarium specimens, make it probable that the "European *biennis*" so-called, rather than *O. Lamarckiana,* was the first *Œnothera* introduced into Europe. Herbarium specimens show, however, that forms closely resembling if not identical with *O. Lamarckiana* and *O. rubrinervis,* formerly occurred wild in the western region of Colorado and New Mexico, and that other forms which, from their flower characters, must be closely related to *O. Lamarckiana* also occur there even now.

Granting that *O. Lamarckiana* must have undergone crossing in its ancestry, it does not necessarily follow that it has been synthesized by a single cross, such as *O. grandiflora* × *O. biennis.* The fact that the characters of the parents are usually blended in crosses between Linnæan species of *Œnothera,* while *O. Lamarckiana* agrees with *O. biennis* in certain bud characters and with *O. grandiflora* in certain other flower characters, does not favor the hypothesis that *O. Lamarckiana* originated from this cross; and the evidence offered by Davis is not supported by a sufficiently critical study of the characters of the three species concerned, the flowers of his hybrids being little more than half the size of ordinary *O. Lamarckiana* flowers. By selecting certain other

races of *O. biennis* for crossing with *O. grandiflora,* hybrids more closely resembling *O. Lamarckiana,* at least in foliage, could doubtless be obtained. It would appear that, as far as the characters are concerned, the "European *biennis*" is as likely to have originated by a cross between *O. biennis* and *O. Lamarckiana,* as *O. Lamarckiana* is to have originated from *O. grandiflora* × *O. biennis.*

From the evolutionary standpoint, however, the important question is not whether a given "species" has arisen through crossing, because this is the condition under which the evolution of open-pollinated species must have taken place. Whether or not we assume that mutation is the result of previous crossing, it is necessary to determine whether the new types which appear are progressive and will form races which will become in turn the progenitors of future types.

Even if it be assumed that *O. Lamarckiana* originated from a cross between *O. grandiflora* and *O. biennis,* such crosses must have occurred in nature in North America centuries before the advent of the white man. For there is ample evidence that both these species originally occupied the Virginia-Carolina region.

The natural and necessary tendency of systematists and collectors is to abstract a few from many existent types, as the foundation for their species. The result is that the actual limits between Linnæan species appear well-defined until the discovery of intermediate races bridging such gaps makes it appear that, in many cases at least, the lines drawn between Linnæan "species" are purely arbitrary. This is shown by cultures of many races belonging to *O. biennis* L. and *O. muricata* L. from various parts of North America.

One piece of negative evidence which does not favor the hypothesis that *O. Lamarckiana* originated from *O. grandiflora* × *O. biennis,* is the fact that none of the mutants from *O. Lamarckiana* have hitherto shown any tendency to revert to either of the putative parents, but

rather, all seem to agree with *O. Lamarckiana* in a certain constellation of flower characters. From plants from garden seeds, however, which have evidently undergone crossing (*e. g., O. suaveolens* from the Nantes Botanical Garden), I have occasionally obtained "mutants" with large petals and short styles.

It seems that the mutation phenomena in *O. Lamarckiana* are due to a disturbed or unstable condition of the germ plasm, which has probably resulted from crossing in the ancestry. It is not probable, however, that the retrogressive mutants, such as *O. nanella* and *O. lata* are due to simple hybrid splitting of types which entered into the ancestry. The chromosomal irregularities during meiosis (maturation), which I described, furnish a possible basis for the occasional appearance of retrogressive mutants in each generation.

Certain cases, however, can not be explained as the result of hybrid splitting or loss of characters, and show that *O. Lamarckiana* has experienced a more general disturbance of its germ plasm. Of these cases, *O. gigas* with its tetraploid number of chromosomes, probably originated through a germinal change at another point in the life cycle. A number of tetraploid species among angiosperms and ferns have probably originated in an analogous manner. Also *O. rubricalyx,* a mutant from *O. rubrinervis* showing a large positive variation in red pigment productions, is not likely to have originated through a new chromosome combination, but more probably through some quantitative cytoplasmic change.

Mutation in *O. Lamarckiana,* therefore, appears to be a condition of germinal instability and not a simple process of hybrid splitting, although this condition of instability has probably been brought about through previous crossing in the ancestry. There is, however, at present no satisfactory evidence that *O. Lamarckiana* has originated from a single cross.

Mutation, whether or not always preceded or accompanied by crossing (of which it is probably a result),

will thus account for much species formation, and for the polymorphism of many genera. That it will account for the larger evolutionary trends and for many adaptations, remains to be shown.

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